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Aspects of relationships between millepedes, soil texture and temperature in deciduous forests

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With 4 figures

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1. Introduction

In western Europe much more work has been done on single species of millepedes, and on their geographical distribution, than has been done on the synecology of the communities that they form. Some attention has been paid to woodland communities, e.g. Blower & Gabbutt (1964), Blower (1970), Geoffroy (1981a), mainly in terms of population densities and phenology in a single site. A number of authors have made some connection between soil type and millepede distribution, for instance Blower (1955, 1956), Biernaux (1972), Kime (1978) and a large scale analysis of ecological factors is being undertaken in Britain (Fairhurst, Harding & Kime 1983) with the intention of eventually incorporating results from the whole of Europe.

This paper presents the results of a synecological analysis of 19 millipede communities found in deciduous forests in Belgium.

Wauthy & Lebrun (1980) have recently shown that the community patterns of a group of arthropods forming the major part of the soil microfauna *viz.* oribatid mites, can unequivocally be related to the main types of humus (mull, moder, peat). We are going to show that the community patterns of millepedes, which constitute a major part of the edaphic macrofauna, are markedly different from the oribatid patterns, since they may be related to the texture of the soil and temperature data in the sites they inhabit.

2. Methods

2.1. Study sites

Although we now have detailed results from more than 40 sites, this paper is based only on the 19 of these for which we currently have all the mesological data. These sites have been chosen first of all because human influence has been minimal; most of them occur in nature reserves. The sites were also chosen because their vegetation is quite representative of the main phytosociological series found in Belgium.

The listed sites can be divided into two sets, those where the percentage of clay in the soil is well below 25% and those where the percentage is well above 25%. In the first set are the following stations: **1**, Grand-Leez (clay percentage = 10.9); **2**, Houthulst (12.1%); **3**, Marche-les-Dames (12.5%); **4**, Angre (13.7%); **5**, Arquennes (13.7%); **6**, Bohan (15.2%); **7**, Tarciennes (16.5%); 8, Cul-des-Sarts (16.7%); **9**, Ham-sur-Heure (17%); **10**, Angleur (17%); **11**, Sadzot (20.6%). In the second set are: **12**, Crupet (28.4%); **13**, Dourbes (33%); **14**, Froidchapelle (34.1%); **15**, Habay-la-Vieille (35%; **16**, Remersdael (35.6%); **17**, Waillet (38.2%); **18**, Thynes (42.2%); **19**, Malempré (44%).

For six stations (numbers 1, 2, 4, 5, 7, and 9) located to the north of the Sambre-Meuse Trench, i.e. located in the Atlantic province, the mean annual temperature is about 9.5 °C. South of this Trench, where stations 6, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18 and 19 are located, the mean annual temperature is lower, around 8 °C. This difference is more marked in winter, the Southern stations being further from the sea and generally at a higher altitude. One station (number 3, Marche-les-Dames) is situated in the Sambre-Meuse Trench. The temperature figures we use are those given for the climatic stations in the study of Poncelet & Martin (1947).

2.2. Sampling

As this was to be a *preliminary survey* it was decided to sample a wide variety of woodland sites, in order to find the abundant species, and to look for any evident relationships between different types of stations and the species found in them.

Each site was searched for about an hour; this searching was usually limited to the litter layers and beneath fallen timber or other objects such as large stones, and beneath the bark of rotting branches. Then a number of soil samples, together with the litter layers, were taken from an undisturbed area. The samples were cut with a knife to have a length of 25 cm and a width of 20 cm ($0.05\ m^2$), and were dug out with a trowel to a depth of approximately 10 cm into the soil below the litter. This depth was not very exact in some of the stations where the ground was very uneven, rocky or full of the burrows of small mammals. Normally, six such samples were taken at different points in the station, taking into account the most important different types of cover within it and representing an area of $0.3\ m^2$; sometimes more samples were taken. Abundances were worked out per 100 kg dry mass of soil. Any species which had been found in the search but not in the samples was allocated a frequency of one individual per 100 kg. 42 stations were sampled between 25th September 1977 and 27th February 1982. Summer sampling was avoided since most species were hardest to find and there were many immature stadia difficult or impossible to identify. Nor was collecting undertaken during cold winter periods when the ground was frozen, so that collecting took place in autumn, spring and mild winter conditions when millepedes were active. This may have led to some bias in the results, for instance *Ommatoiulus sabulosus* (L.) is known to be more active in summer, and many iulids, glomerids and particularly blaniulids descend into the soil below the sampling depth in winter. On the whole most species present in the forests should have been found in the samples when they were taken, but it is realized that the degree of sampling was not sufficient to locate species of a very low density except by chance. Some sites, numbers 6, 7, 9, 10, 12, 15, 16 and 17, were sampled in successive years and at different seasons. These repetitive visits indicated that on the whole the same main species were found each time, and that some species were not encountered in midwinter. For sites quantitatively sampled on more than one occasion we give the mean value for each species density.

2.3. Numerical Analysis

2.3.1. Community Analysis

The aim of community analysis is to discover which identical environmental conditions bring about identical community structures. A lot of techniques may be used (for a recent review, see Noy-Meir & Whittaker 1977). In this instance we use correspondence analysis, i.e. an "ordination" technique in the normally accepted sense. The purpose of correspondence analysis is to arrange communities and species along axes, allowing these axes to be interpreted as "environmental gradients" that can be related to one or more ecological variables (Whittaker 1978).

2.3.2. Patterns of distribution

In practice, these ecological variables constitute the fundamental parameters of the niches occupied by the species, at least with regard to their spatial aspects. The variables provide an informative framework within which the spatial patterns of *community distribution* can be described. If we consider the arrangement of the communities along the gradients defined by the variables, the γ-diversity measure will show the number of occupied niches and the regularity with which this number increases (for details, see Blondel 1979). These variables can also be investigated in terms of possible habitat "resources" for the species. In this context, as Lynch (1981) proposes, we can establish for each species a level of habitat specialization defined by these resources. This is a less global approach than the previous one, since it refers to *species distribution* in response to some identified variables.

2.3.3. Preferenda analysis

In order to complete our synecological approach to millepede communities we need to establish those variables for which some species have the greatest indicatory power. At the present time the best method is to analyse the "mean mutual information" between variables and species (see Daget *et al.* 1972). But this method, if it is to be valid, requires a much larger number of sites than we have (Lepart, pers. com.). Therefore we have followed the suggestion of Bonnet (1978) in establishing the ecological preferenda of each species, and have compared these preferenda using the multiple correspondence analysis of Lebart *et al.* (1977) (for further details, see Wauthy 1982).

The distribution of each species corresponds to its preference for a low **(1)**, high **(3)** or intermediate **(2)** level of each variable. We have also taken into account the population density in the following way: if the density in a given site is greater than the mean density in all the sites, we count this site twice in assessing the species distribution.

2.4. Mesological variables

Not only have temperature data and measures of soil texture been taken into account, but other variables that might be related to different millepede densities, or different composition of the millepede communities (see Blower 1956, Barlow 1957, Kendeigh 1979, among others).

Three variables, referring to physical and chemical conditions in the soils, are studied from a qualitative point of view, i.e. the internal drainage, the thickness of the organic horizons and the amount of active calcium:

- the first variable is studied in the same way as Wauthy (1981) indicates;
- the listed organic horizons are divided into four classes of increasing thickness, with the following simple values: (i) **1**, for calcic mull organic horizons (sites 3, 12, 13, 16 and 18); (ii) **2**, for non-calcic mull horizons (sites 4, 5, 6, 7, 11, 14, 15 and 17); (iii) **3**, for moder horizons (sites 1, 2, 8, 9 and 10); (iv) **4**, for peat soil (site 19);
- the soils are divided into three active calcium classes, with the following simple values: (i) **2**, for calcimagnesic soils (sites 3, 12, 13, 16 and 18); (ii) **1**, for soils with a good reserve of bases (sites 5, 7 and 15); (iii) **0**, for all other cases.

Two variables are listed in terms of quantitative data. They refer to chemical conditions (nitrogen percentage) and topographical conditions (altitude).

3. Results and discussion

3.1. Faunistical aspects

Belgium is an interesting country with regard to millepede distribution since it lies at the edge of the known geographical range of many species, indeed this study has extended the known range of some species to include Belgium for the first time. The most recent reviews of the fauna are those of Biernaux (1972) for the order Iulida, and before that of de Queker (1962) for all species recorded in Belgium up to that date. Only Biernaux (1972) provides information about ecological preferences. Since Belgium is a sort of "cross-roads" we have given much attention to climatic data, where small differences might in the end be important. There are "Atlantic" species such as *Polydesmus coriaceus* Porath (= *gallicus* Latzel), *Leptoiulus kervillei* (Broelemann) and *Leptoiulus belgicus* (Latzel) which have in Belgium so far been found only in the Atlantic province and are at or near to the north-eastern limit of their range; other Atlantic species are found more widely in Belgium and extend into the Sub-Atlantic submontane areas, such as *Melogona gallicum* (Latzel) (the most numerous millepede in our survey) and *Polydesmus testaceus* C. L. Koch. On the other hand there are "Continental" species such as *Melogona voigti* (Verhoeff), *Orthochordeuma germanicum* (Verhoeff) and *Enantiulus nanus* (Latzel) which reach their western limit in Belgium. *Orthochordeumella pallida* (Rothenbuehler), *Glomeris connexa* C. L. Koch and *Craspedosoma alemannicum* Verhoeff reach their north-western limits, and *Chordeuma silvestre* C. L. Koch, *Ceratosphys amoena* Ribaut and *Glomeris hexasticha* Brandt *intermedia* Latzel are the at northern end of their range.

Many observations have been made in the past concerning the types of soil that millepedes whose range includes Belgium prefer (see, for instance Blower 1955, 1956, Biernaux 1972). Certain species e.g. *Ommatoiulus sabulosus* (L.) and *Cylindroiulus latestriatus* (Curtis) are associated with sandy soils, others e.g. *Cylindroiulus nitidus* Verhoeff and *Blaniulus guttulatus* (Bosc) with heavier silts, clays or "limon". A number of wide ranging species have been thought to reach their maximum densities on sandy soils (e.g. *Iulus scandinavius* Latzel) or on shallow calcareous soils [e.g. *Tachypodoilus niger* (Leach) (= *albipes* C. L. Koch) and *Glomeris marginata* (Villers)], whilst others are considered to be strictly calcicole e.g. *Archiboreoiulus pallidus* (Brade-Birks), *Polydesmus testaceus* C. L. Koch, *Geoglomeris jurassica* Verhoeff, *Macrosternodesmus pallicola* Broelemann. Blower (1955) suggested that chordeumatids and polydesmids (flat-backs) that do not burrow will tend to inhabit thick protective litter layers (on well-drained soils?) since they are susceptible to wetting and water uptake just as they are susceptible to desiccation. Iulids are more resistant, and able to burrow, for which purpose a sandy soil will be more advantageous, though loams and crumbly clays or clays with earthworm burrows or other holes are not precluded.

Table 1. Distribution and population densities of millepedes per 100 kg of dry matter in 19 deciduous for-

		Stations														
		Grand-Leez	Houthulst	Marche-les-Dames	Angre	Arquennes	Bohan	Tarciennes	Cul-des-Sarts	Ham-sur-Heure	Angleur	Sadzot	Crupet	Dourbes	Froidchapelle	Habay-la-Vieille
1.	*Polydesmus denticulatus*	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
2.	*Ceratosphys amoena confusa*	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
3.	*Geoglomeris jurassica*	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4.	*Glomeris marginata*	0	0	0	0	0	0	0	0	0	58	0	0	0	0	0
5.	*Blaniulus guttulatus*	0	0	0	0	1	0	0	0	0	0	0	280	0	0	0
6.	*Cylindroiulus punctatus*	62	0	0	1	9	0	0	0	0	0	0	0	0	0	0
7.	*Archiboreoiulus pallidulus*	0	0	0	0	0	0	0	0	1	0	0	27	0	0	0
8.	*Leptoiulus kervillei*	0	0	249	0	0	0	0	0	0	0	0	0	0	0	0
9.	*Iulus scandinavius*	0	1	0	1	1	0	0	0	0	0	0	0	0	0	1
10.	*Polydesmidae* sp.	0	0	0	0	0	0	24	0	0	0	0	0	0	0	11
11.	*Polydesmus angustus*	0	0	0	1	9	45	1	0	1	1	0	0	0	0	0
12.	*Orthochordeumella pallida*	0	0	31	0	30	261	0	0	77	1	0	1	0	23	0
13.	*Tachypodoiulus niger*	0	0	31	1	0	0	0	0	1	0	1	60	0	0	0
14.	*Glomeris hexasticha intermedia*	0	0	0	11	0	1	0	0	0	23	0	193	89	0	0
15.	*Cylindroiulus nitidus*	0	0	16	0	0	0	0	0	13	0	0	107	310	47	11
16.	*Macrosternodesmus palicola*	0	0	31	0	0	0	0	0	0	0	0	107	15	0	0
17.	*Brachydesmus superus*	124	52	109	11	0	364	0	0	77	1	1	0	0	0	0
18.	*Craspedosoma rawlinsi* & *C. alemannicum*	1	78	0	1	1	57	182	0	26	127	0	1	0	1	1
19.	*Chordeuma silvestre*	0	0	0	0	10	125	24	28	65	80	75	0	30	0	11
20.	*Melogona gallicum*	0	52	16	741	86	387	0	0	413	310	15	233	30	140	0

The limit values concerning low (1), intermediate (2) and high (3) conditions of these variables are indicated, column indicates the species specialization on clay percentage and mean annual temperature habitat.

3.2. Community analysis

3.2.1. Sampling results

The species richness varies considerably from one site to another, only one species having been found in station 8 (Cul-des-Sarts) and 12 species in station 16 (Remersdael) (One of the 23 stations not included in the present analysis yielded 15 species). Assuming that the distribution of species is not entirely a matter of chance, but determined by certain environmental conditions, the correspondence analysis of faunal assemblages effected by the millepedes in the sites must provide "eigenvalues" with inertia rates higher than those measured by Lebart *et al.* (1977) on completely randomized data matrices.

est stations, on which species preferenda are computed for 11 environmental variables

				Preferenda for environment variables											
Remersdael	Waillet	Thynes	Malempré	Soil clay percentage (**1**: 13.7—18.9; **2**: 20.2—24.6; **3**: 25.8—35.6)	Soil silt percentage (**1**: 33.4—55.5; **2**: 55.9—61.3; **3**: 62.0—77.3)	Soil sand percentage (**1**: 9.0—17.9; **2**: 18.3—19.0; **3**: 19.1—31.0)	Mean annual temperature (**1**: 8.3—8.7; **2**: 8.7—8.8; **3**: 8.9—9.5)	Minimum monthly temperature in winter (**1**: —9.5— —8.9; **2**: —8.9— —8.7; **3**: —8.7— —7.1)	Maximum monthly temperature in summer (**1**: 28.7—28.9; **2**: 29.0—29.3; **3**: 29.3—29.6)	Soil moisture (**1**: 1.0—1.3; **2**: 1.6—2.0; **3**: 2.0—3.0)	Soil nitrogen percentage (**1**: 0.6—0.8; **2**: 0.8—0.9; **3**: 0.9—1.1)	Tickness of organic horizons (**1**: 1.0—1.6; **2**: 1.7—2.0; **3**: 2.0—3.0)	Altitude (**1**: 92—178; **2**: 179—191; **3**: 196—254)	Soil active calcium (**1**: 0.0—0.5; **2**: 0.5—1.2; **3**: 1.3—2.0)	Specialization on habitat (**1**: low; **2**: intermediate; **3**: high)
0	0	0	0	1	3	1	3	3	1	2	1	2	1	1	3
0	0	0	0	1	3	2	2	2	3	3	2	3	1	1	3
34	0	0	0	3	1	3	2	2	3	1	1	1	2	3	3
11	0	1	0	3	1	3	2	1	3	2	2	2	2	2	3
66	0	0	0	3	1	2	2	2	3	1	1	1	1	3	3
1	0	0	0	1	3	1	3	3	2	3	3	2	1	2	3
0	0	0	0	2	2	1	1	1	3	1	1	2	2	3	3
21	0	0	0	2	2	2	3	3	2	1	1	1	1	3	3
0	0	0	0	1	2	3	3	3	1	3	2	2	1	1	2
0	0	0	0	2	3	1	3	3	1	3	3	2	3	2	2
0	0	1	0	1	3	1	1	2	1	2	3	2	2	2	2
0	0	0	0	1	3	2	1	1	2	2	2	3	3	1	2
11	0	12	0	2	2	1	2	2	2	1	2	1	2	2	2
0	19	0	0	3	1	2	1	1	2	2	1	1	2	2	2
284	0	410	0	3	1	1	1	1	2	1	2	1	2	3	2
1	0	0	0	3	1	2	2	2	3	1	1	1	1	3	2
75	0	1	0	1	2	3	2	3	1	2	3	2	2	1	1
1	1	12	1	2	1	3	2	2	2	3	3	3	3	1	1
1	1	24	39	2	2	2	1	1	1	3	3	3	3	1	1
216	0	133	78	2	2	3	1	1	1	2	2	2	3	2	1

in brackets. Unities referring to some variables are specified in section "Materials and methods". The last categories.

If the data matrix (20 × 19) takes into account merely the presence or absence of each species in the sites the inertia rates of the first two eigenvalues are 18.4% and 13.8% respectively, i.e. a little below the relating thresholds computed by LEBART *et al.* (1977) *viz.* 21% and 16% respectively. However, if we take the densities of the millepede populations into account, in other words, the way in which each site environment influences the local populations, the inertia rates become much higher, whether the abundances are expressed as millepedes per m^2 or per 100 kg (dry mass) of sampled material; and, because the inertia rates are higher in the latter case (23.6% and 18.1%, respectively), we are quantifying the populations discussed in this paper using the number of individuals per 100 kg (dry mass; Table 1).

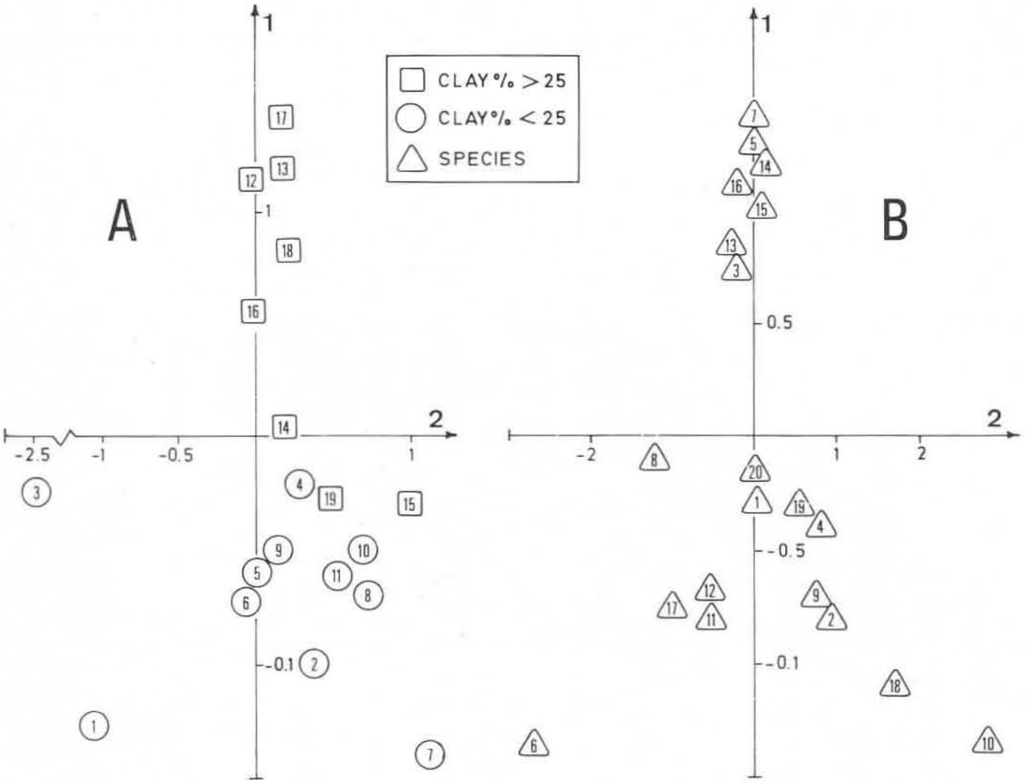

Fig. 1. Binary correspondence analysis of 19 community samples made on 20 species of millepedes in deciduous forests. Abundances are expressed in number of individuals for 100 kg of dry matter. **(A)** community location in the space of axis 1 and 2. Station origin of communities: **1**, Grand-Leez; **2**, Houthulst; **3**, Marche-les-Dames; **4**, Angre; **5**, Arquennes; **6**, Bohan; **7**, Tarciennes; **8**, Cul-des-Sarts; **9**, Ham-sur-Heure; **10**, Angleur; **11**, Sadzot; **12**, Crupet; **13**, Dourbes; **14**, Froidchapelle; **15**, Habay-la-Vieille; **16**, Remersdael; **17**, Waillet; **18**, Thynes; **19**, Malempré. **(B)** species location in the space of axis 1 and 2. Numbers designating species are identical with those on table 1.

As far as the locations of the communities in the space of the first two axes of the correspondence analysis are concerned, the only important differences that can be seen between the presence-absence data matrix and the abundance/100 kg data matrix relate to the situations of Marche-les-Dames, Waillet and Thynes (sites 3, 17 and 18 respectively). The overall similarity of the results indicates that the ordinations defined by the first two axes cannot be put down to simple fluctuations in the sampling.

3.2.2. Axis interpretation

As shown in figure 1A, the arrangement of the communities along the first axis corresponds to the heaviness of the soil although the order of the stations does not exactly coincide with the increasing gradient of soil clay content. The communities at Crupet (no. 12; soil clay % = 28.4) and Tarciennes (no. 7; soil clay % = 16.5) contribute the most to the creation of the axis (the values of absolute contribution are 28% and 10% respectively).

It might be considered anomalous that among the five communities closest to the centre of gravity, there are three found on heavy soils (no. 14, Froidchapelle, no. 15, Habay-la-Vieille; no. 19, Malempré) and two living on lighter soils (no. 3, Marche-les-Dames; no. 4, Angre). The presence in this set of station no. 3 may be explained by the fact that the soil there is the sole listed calcimagnesic soil with a low percentage of clay (12.5%); the four other soils of this type are much heavier (clay % > 28) and are situated well above the centre of gravity. This is not the case with station no. 4, but this is the one community to have been prospected late in the spring (25. V. 80) when it was numerically dominated by young stadia of *Melogona gallicum*, the most ubiquitous of the species we found.

The arrangement of the species along the first axis (fig. 1B) also relates to the soil clay percentage. The two taxa which most contribute to the formation of the first axis are *Cylindroiulus nitidus* (no. 15; absolute contribution = 28.3%) and the *Craspedosoma rawlinsi* + *C. alemannicum* group (no. 18; absolute contribution = 14%); *C. nitidus* is numerically dominant or largely sub-dominant in most stations where the soil is rich in clay; on the other hand the *C. rawlinsi* — *C. alemannicum* group has a more ubiquitous distribution, but is dominant or largely sub-dominant on soils poor in clay, notably at Houthulst (station no. 2), Tarciennes (no. 7) and Angleur (no. 10) (*Craspedosoma rawlinsi* and *Craspedosoma alemannicum* were grouped because in many stations no adult males were found and it was impossible to refer the animals to either species. Both species are well represented in Belgium but their distribution remains to be worked out).

The first axis isolates a set of seven species (nos. 7, 5, 14, 16, 15, 13 and 3) above the gravity centre. These species are all well represented in stations containing a high percentage of clay in the soil and include *Cylindroiulus nitidus*, *Geoglomeris jurassica*, *Glomeris hexasticha*, *Blaniulus guttulatus*, *Archiboreoiulus pallidus*, *Macrosternodesmus palicola* und *Tachypodoiulus niger*. Apart from *M. palicola* those are all glomerids or iulids that can roll up and/or tunnel, the majority are calcicole and some are believed to be xerophilous. In the climatic conditions prevailing in Belgium the calcimagnesic soils in forests very often have a high percentage of clay particles and a very variable water content with the possibility of prolonged periods of drought in summer (Duchaufour 1977).

The interpretation of the second axis is less obvious than that of the first. When the presence-absence data matrix is used the position of just one species, i.e. *Leptoiulus kervillei* (no. 8), is very different from its position on the abundance/100 kg data matrix Therefore, as Volle (1981) indicates, this species is considered as an "illustrative element" of the correspondence analysis shown in figure 1B; thus, *L. kervillei* does not intervene in the computation of the space location of the other species, but its location depends upon them.

When the communities are considered, those contributing the most to the formation of the second axis are Tarciennes (no. 7; relative contribution = 40%) and Grand-Leez (no. 1, relative contribution 29.5%); but we have not been able to relate the order of the communities along the axis with respect to the ecological variables that we considered.

When we consider the species, the two taxa which contribute most to the second axis, on which their location is also the most distant, are *Craspedosoma rawlinsi* & *C. alemannicum* (no. 18; relative contribution = 39.2%) and *Cylindroiulus punctatus* (no. 6; relative contribution = 18.7%), and these two taxa have very different thermal requirements. Indeed, Haacker (1968) gives the thermal optimum of *C. alemannicum* as between 0 and 8 °C, while it is from 18 to 26 °C in the case of *C. punctatus*. *C. rawlinsi* has been recorded much more frequently in the North of Britain than in the South (British Myriapod Group records from Fairhurst, pers. comm.) and is active in winter so it is not unreasonable to suppose that it also has a low optimum temperature range. Although we do not have data for temperature preferences of many species, we have examined the data and opinions of many authors and have considered the geographical distribution of all the species we recorded in conjunction with climatic criteria. We find that species that are typically calcareous are located to the left of the centre of gravity, with *C. punctatus*. As the temperatures in calcimagnesic forest soils are often high in summer it would not be surprising if the species in them had a preference for such temperatures, as does *Tachypodoiulus niger* (18 to 26 °C according to Haacker 1968) which is common on such soils and also found to the left of centre of the second axis. On the other hand, to the right of the centre of gravity, we find, with *Craspedosoma*, species such as *Chordeuma silvestre* and *Iulus scandinavius* which are active in winter and/or have a continental distribution, the "non-Atlantic" species. *C. silvestre* is a submontane species on the continent, and *I. scandinavius* is a "northern" species which extends south west only into nothern, central and mountanous eastern France, in which it resembles *C. silvestre* (DEMANGE 1981).

Finally, it can be said that a thermal interpretation of the second axis seems reasonable. We have not tried to interpret any further axes because their inertia rates are lower than the associated thresholds of significance.

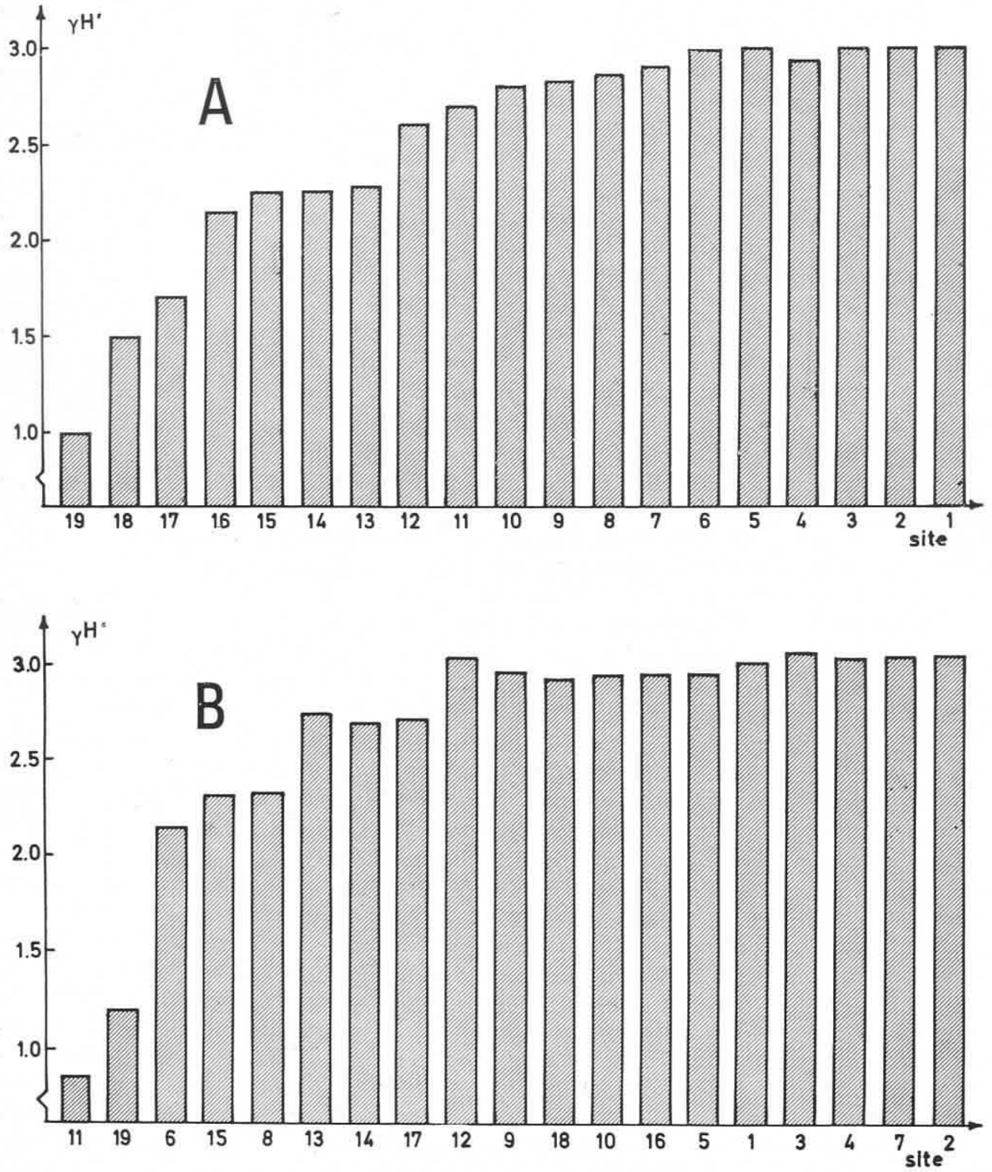

Fig. 2. Gamma diversity evolution of 19 millepede communities. **(A)** Along a decreasing gradient of soil clay percentage. **(B)** Along an increasing gradient of mean annual temperature.

3.3. Patterns of distribution

3.3.1. Cumulative diversity

The relationship between soil clay percentage or temperatures in the listed sites and the numerical structure of millepede communities which are evolving within these sites can also be illustrated using "cumulative" gamma diversity defined by Blondel (1979).

Blondel (1979) suggests that diversity within a collection of communities arranged in a "logical" way (for example, along any mesological gradient) might vary as a function of the number of available habitats that species are able to "accumulate" within the collection. Gamma diversity increases regularly and proportionally as diversities (measured by the Shannon heterogeneity index, and expressed in bits/individual) of the different sites are progressively added and mixed together; finally, gamma diversity leads to a maximum when habitat saturation is achieved by the species.

If we compare gamma diversity established on the soil clay percentage gradient of the listed sites (fig. 2A) to the ones calculated on gradients referring either to physical variables (such as soil silt percentage, soil sand percentage, water content fluctuations within organic horizons) or to chemical variables (such as *p*H, exchange acidity, carbon percentage, nitrogen percentage), the graphs are very different: we can observe either important deviations in the increasing phase of gamma diversity or rapid rises of the stabilization phase.

This is not the case if the comparison concerns several variables referring to site temperature, and particularly mean annual temperature (fig. 2B), minimum monthly temperature in winter and maximum monthly temperature in summer (not represented). On the other hand, we observe the above-mentioned graph irregularities where other climatic data available from Poncelet & Martin's (1947) work (such as number of days without frost, number of days > 5 °C, total annual precipitation) are concerned.

Finally, the results indicate that the most "harmonious" way in which millepedes utilize the habitat is in correspondence with soil clay percentage and mean annual temperature gradients; but we do not have data about the individual patterns of segregation in the available habitat.

3.3.2. Specialization on habitat

The results of correspondence analysis completed by those of gamma diversity allow us to recognize four possible double modes of utilization of habitat within the listed sites and to divide them into four more or less equal groups. There are: **(1)** habitats referring to soils with low clay percentage (15.2—20.6%) and low mean annual temperature (7.3 to 8.5 °C) (stations n. 6, 8, 9 and 11); **(2)** habitats referring to soils with low clay percentage (10.9—16.5%) and high mean annual temperature (9.2—10 °C) (stations n. 1, 2, 3, 4, 5 and 7); **(3)** habitats referring to soils with high clay percentage (17—42.2% and high mean annual temperature (8.5—8.8 °C) (stations n. 10, 12, 16, 17 and 18); **(4)** habitats referring to soils with high clay percentage (33—44%) and low mean annual temperature (7.3—8.3 °C) (stations n. 13, 14, 15 und 19). Herein, we want to study for each species the diversity of utilization and the level of specialization towards these disjunctive habitat categories.

If we establish the relative abundance of species in each major habitat category, habitat diversity can be summarized in a square diagram (fig. 3A) the corners of which represent the four possible categories. One of the most common habitat utilizations (8 species) corresponds to the lower right sector of the diagram, i.e. to soils with high clay percentage and high mean annual temperature. The presence of the calcicolous species within this set is not surprising since four out of the five listed calcimagnesic soils are rich in clay. In addition it is noticeable that most of the millepedes of this group are able to protect themselves from unfavourable life conditions by means of their form and/or their behaviour. As already indicated, the blaniulids, *Blaniulus guttulatus* (no. 5) and *Archiboreoiulus pallidulus* (no. 7), may go down deep even into compact coils (Biernaux & Baurant 1964, Biernaux 1968). So may *Cylindroiulus nitidus* (no. 15) (Geoffroy 1981b). According to Haacker (1968),

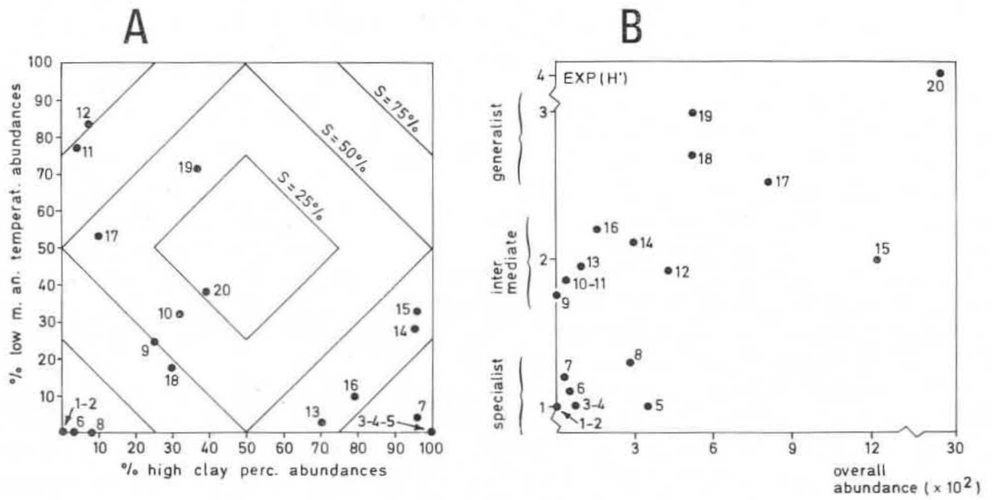

Fig. 3. Diversity on habitat in the 20 millepede species. Numbers designating species are identical with those on table 1. **(A)** specialization on the four major habitat catogories. category n. 1 refers to the upper left corner of the square; cat. n. 2 to lower left corner; cat. n. 3 to lower right; cat. n. 4 to upper right. % high clay percentage abundances = category n. 3 + cat. n. 4; % low mean annual temperature abundances = cat. n. 1% + cat. n. 4%. **(B)** relationship between niche breath on major habitat categories and total species number of individuals.

Tachypodoiulus niger (no. 13) is xerophile and withstands a large temperature range. The Glomerids, i.e. *Geoglomeris jurassica* (no. 3), *Glomeris marginata* (no. 4) and *Glomeris hexasticha intermedia* (no. 14) can roll into a ball; HAACKER (1968) found *G. marginata* indifferent in its responses to humidity. This could be important in skeletal soils, especially in hot, dry summer weather (see BLOWER 1956). *Macrosternodesmus palicola* (no. 16) requires further study; it is a very small, thin polydesmid, which might penetrate into the soil.

The absence of points in the upper right corner of the diagram indicates that millepedes do not favour cold and heavy soil conditions.

The data at our disposal do not allow us to formulate with certainly a common strategy for the eight species plotted in the lower left corner, though most of them live in the litter layers, making a sandy substrate an insurance against waterlogging.

Among the four species that fall within the upper left corner there are two mobile chordeumatid species, i.e. *Orthochordeumella pallida* (no. 9) and *Chordeuma silvestre* (no. 19), active in continental areas in winter, and two polydesmids, *Polydesmus angustus* (no. 11) and *Brachydesmus superus* (no. 17). Here again there is an evident connection between behabiour and life conditions. It seems a reasonable hypothesis to deduce from these observations that the faunal organization of millepede communities is poorly affected by the abiotic environment and its irregularity, i.e. according to KLOPFER's (1959) model of community structuring mechanisms

Habitat specialization can be measured using the S coefficient of LYNCH (1981). In the present case, S = abs. (% low mean annual temperature abundances —50) + abs. (% high clay percentage abundances —50). Eight species (nos. 1, 2, 3, 4, 5, 6, 7 and 8) can be considered as *very specialized* on the defined habitat categories, since their S coefficient is well over 75%; three of them (nos. 1, 2 and 3) are restricted to only one habitat. On the other hand, four taxa (nos. 20, 19, 17 and 10) could be considered as *weakly specialized* (S coefficient well below 50%); they have significant abundances in at least three habitat categories, except for the *Polydesmidae* taxon which consists of unidentifiable young stadia of large polydesmids, and which is likely to be entirely or very largely *P. angustus*, and so is artificial. A third group is comprised of four "intermediate" specialized species (nos. 13, 14, 15 and 16), with *S* coefficients well between the 75% and 50% limit values; to these species may be added the four species whose specialization values are more or less equal to the limiting values (i.e. taxa no. 9 = 50%, no. 18 = 52%, no. 11 = 73% and no. 12 = 77%; but note that the real value of no. 11 may be lower if it includes members of taxon 10).

In order to establish the specialist-generalist status of these four latter species, our interpretation of the *S* coefficient must take into account at one and the same time the local abundances and the number of occupied sites. Indeed, a species that is encountered in several sites may appear to have a weak specialization on habitat if it is locally very abundant. The exponential form of the Shannon function $[\mathrm{EXP}(H') = \mathrm{EXP}(-\sum p_i \ln p_i)]$ is used in order to express the local species abundances, where p_i = the relative abundance of a given species in the ith major habitat category. A species with $\mathrm{EXP}(H') = 4$ is a perfect generalist and, according to the Hutchinsonian concept, one can say that its "niche breadth" on defined habitat is very great. No such species exists among the group studied. On the other hand, a species with $\mathrm{EXP}(H') = 1$ is a specialist, but great scatter is evident.

In fact, if niche breadth is plotted against overall abundance (fig. 3B), it can be seen that the species may be grouped in three categories which correspond to a considerable extent to the sets defined above using *S* coefficient. But there are some exceptions: the location of the *Craspedosoma rawlinsi* — *C. alemannicum* group (no. 18) leaves no doubt about its generalist status; on the other hand, despite its nearly identical *S* coefficient (± 50%), *Iulus scandinavius* (no. 9) is located in the "intermediate" set; this is not surprising since the latter species was encountered four times less often and in much smaller numbers (4 *versus* 491 individuals). This also applies to *Polydesmus angustus* (no. 11) and *Orthochordeumella pallida* (no. 12) although their specialist trends are marked in figure 3A ($S \simeq 75\%$); but they were encountered in quite a large number of sites (7 each). Note too that in figure 3B species 10 and 11 fall together; as above mentioned, this suggests that the unidentified polydesmids were *P. angustus* and that the species occurred in eight sites.

Fig. 3B also indicates that more abundant species tend to more largely utilize the habitat. This appears to be a fairly general phenomenon (see LYNCH 1981, for discussion). If we consider the two most abundant species in our samples, *Cylindroiulus nitidus* (no. 15; overall abundance = 1,198 ind.) has an *S* value of 63%, whereas the commonest species, over twice as abundant as this, *Melogona gallicum* (no. 20; overall abundance = 2,850 ind.), has a *S* value of 23%, over twice as low. In another connection, two species, i.e. *Blaniulus guttulatus* (no. 5) and *Leptoiulus karvillei* (no. 8), which both belong to the group of specialists, are very abundant in one of the four major habitat categories (346 ind. in cat. no. 3 and 249 ind. in cat. no. 2, respectively). For this reason they can be regarded as "super-specialist" on habitat. We must qualify this statement with regard to *B. guttulatus* since it is possible that we sampled stations where it was too deep in the soil to be collected at the time. On the other hand, it is quite possible that in natural forest habitats, as opposed to cultivated areas, it is a specialist, preferring relatively high clay content, high calcium and warmer soils.

3.4. Preferenda analysis

3.4.0. General

For each species, preferences for environmental variables can be expressed using the following simple values: **(1)** when the species distribution is related to "low" conditions of the variables; **(2)** for "intermediate" conditions; **(3)** when the distribution is related to "high" conditions. Table 1 first presents species preferenda for the soil clay percentage variable and for two other variables, i.e. silt percentage and sand percentage, which classically intervene in the soil texture analysis, and second, species preferenda for climatic variables which relate to the numerical structure of millepede communities as mentioned above.

3.4.1. *Specialization on habitat in relation to ecological preferenda*

In table 1, we also use simple values in order to assign to each species one of the three above-defined increasing levels of specialization on habitat (see last column of Table 1). The first question we ask is whether the species belonging to the same specialization level have identical preferenda. To this end (see WAUTHY 1982), multiple correspondence analysis has been used and fig. 4 presents location results of the three specialization levels, the nine texture conditions and the nine climatic conditions in the first two multiple axes. The other axes have not to be considered because the inertia rates (25.2% and 17.5%, respectively) associated with the first two eigenvalues (computed values are 0.50 and 0.35, respectively) are high compared with the relatively small dimensions of the data matrix (20×21). Five other variables, to which millepede distribution and community structure are commonly related (see section 2.4) have been used as "illustrative elements" within the multiple correspondence analysis (see LEBART *et al.* 1977, for theoretical details) and are also plotted in the plan of axes 1 and 2.

The levels of specialization on habitat greatly contribute to the creation of axis 2 (cumulated absolute contribution = 26%). Moreover, the three points referring to these levels fall into a line nearly perpendicular to axis 2 (line with alternating points and strokes on fig. 4), while no such alignment can be observed for any single environmental variable. This means that from a global point of view the species preferenda are very varied within each level of specialization.

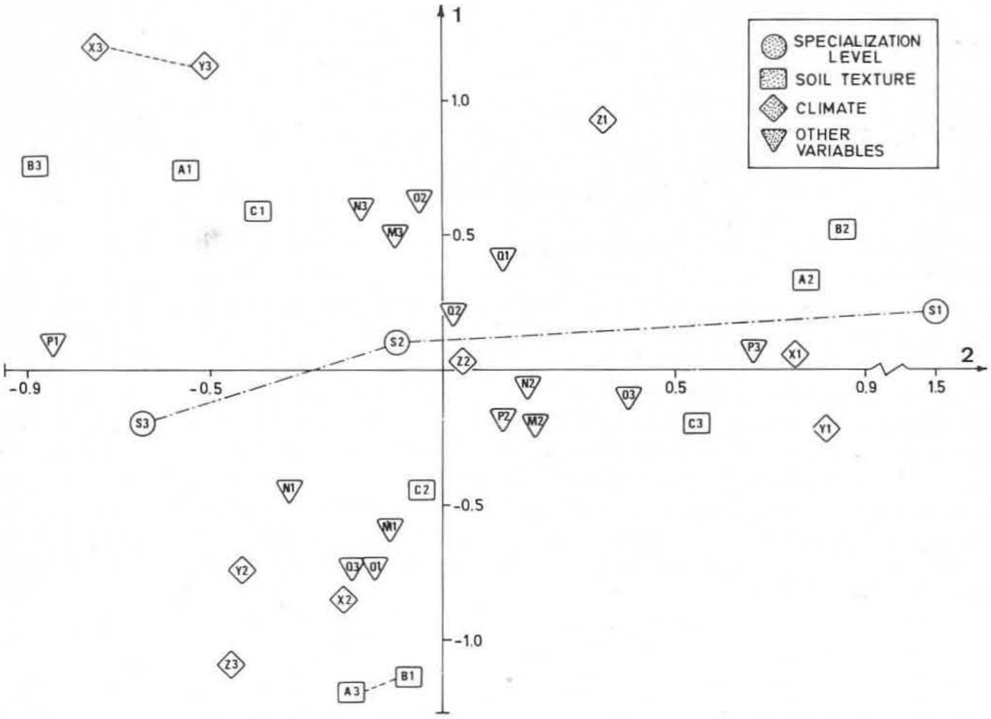

Fig. 4. Multiple correspondences analysis of 3 levels of specialization on habitat, 18 descriptive elements referring to soil texture and climate preferenda and 15 illustrative elements referring to preferenda for 5 other environmental variables, defined on 20 millepede species. Plan of axes 1 and 2. Line with alternating points and strokes refers to the 3 specialization levels; dotted lines join the four elements which most contribute to the first axis creation. **(A)** soil clay percentage; **(B)** soil silt percentage; **(C)** soil sand percentage; **(X)** mean annual temperature; **(Y)** minimum monthly temperature in winter; **(Z)** maximum monthly temperature in summer; **(M)** soil moisture; **(N)** soil nitrogen percentage; **(O)** thickness of organic horizons; **(P)** site altitude; **(Q)** soil active calcium.

There is also the suggestion of an interesting and plainly logical conclusion that probably could be applied more generally to other taxonomic groups of soil fauna: among millepedes, the generalists with respect to the defined habitat trends are species with *similar enough* behaviour towards the environment; inversely, the specialists are species with *very particular* behaviour towards the environment.

In fact, examination of species preferenda indicates that in the "best" cases (i.e. for maximum monthly temperature in summer and for altitude) no more than 3/4 of the species have identical preferenda. Let us give details for maximum monthly temperature in summer: three generalist on habitat species (nos. 17, 19, 20) out of four prefer "low" conditions of the variable (Z1); four species with intermediate status (nos. 12, 13, 14, 15) prefer "intermediate" conditions; and, five specialists (nos. 2, 3, 4, 5, 7) out of eight prefer "high" conditions (Z3). The same detail for altitude is: 3/4 generalists (nos. 18, 19, 20) prefer "high" conditions (P3); 4/8 intermediate species (nos. 11, 13, 14, 15) prefer „intermediate" conditions; and 5/8 specialists (nos. 1, 2, 5, 6, 8) prefer "low" conditions (P1). Nevertheless, where the whole eleven studied variables are concerned, it appears that the specialist species have *relatively fewer* identical preferenda than the other species. More precisely: 3/4 generalist species have a similar prederendum for seven variables (A, B, C, Z, N, P, Q); 4/8 intermediate species have a similar preferendeum for seven variables (C, X, Z, N, O, P, Q); and, only 3/8 specialists have a similar preferendum for eight variables (A, B, C, X, Y, M, O, Q).

3.4.2. Indicative value of millepedes

After indicating and analysing the predictive value of soil clay percentage and mean annual temperature on the numerical structure of millepede communities, we must now inversely study the predictive value of species first on these variables and their associated conditions, and second, on field variables to which numerical structure is usually referred. Nevertheless, such a study implies sampling a greater number of sites than the present one. Therefore, we shall indicate for which variables an intensive and contrasted site sampling will be necessary and adequate in the future.

With this end in view, the results of multiple correspondence analysis bring out two important aspects:

(1) The environmental conditions which most contribute to the creation of the first axis and at the same time are very distant from the gravity centre refer to high clay percentage and low silt percentage (points A3 and B1, respectively, joined by a dotted line on fig. 4; absolute contribution = 13% and 13.2%, respectively). Six species, i.e. *Geoglomeris jurassica, Glomeris marginata, Blaniulus guttulatus, Glomeris hexasticha int., Cylindroiulus nitidus* and *Macrosternodesmus palicola*, make an important group, not only as they have identical preferenda for both above-mentioned contrasted conditions, but also as they have, globally speaking, a great number of identical preferenda for the other environmental conditions. If we consider the second possibility of contrast between clay and silt percentages, i.e. low clay % (A1) and high silt % (B3), five species are concerned; these are: *Polydesmus denticulatus, Ceratosphys amoena confusa, Cylindroiulus punctatus, Polydesmus angustus* and *Orthochordeumella pallida.*

This separation into two distinct groups each containing a number of common species probably means that the indicative power of millepedes towards *contrasted conditions* of soil clay and soil richness is very great.

(2) Two other environmental conditions, i.e. high mean annual temperature and high min. monthly temp. in winter (X3 and Y3, respectively), with high absolute contribution (10.4 and 10.8%, respectively) are located towards the first axis on the opposite side of A1 and B3 conditions. This location indicates that the concerned species are, by no means, all the same as the ones concerned by the latter conditions; these are: *Polydesmus denticulatus, Cylindroiulus punctatus, Leptoiulus kervillei, Iulus scandinavius* and *Polydesmidae Gen.* sp.

This means that in the future we might probably expect that very few species have great indicative value at one and the same time for textural and climatic parameters.

4. Conclusions and future prospects

If relationships between millepedes, temperature and humidity have been stressed in several works, and other, often biotic, factors have been considered, those referring to soil texture, and particularly to soil clay percentage, were rarely indicated, with the exception of some detailed works on mainly iulid species which we have referred to. Our present knowledge allows us to consider the significance of clay in a number of ways:

(1) As opposed to "flat-back" millepedes, the iuliform species (except in practice some epigeous species) constitute a guild in Root's meaning (1967), because of their ability to modify the physical structure of the soil by burrowing (see Jeanson 1980). Glomerids may also burrow. The resistance towards burrowing evidently depends on soil compactness. And, generally speaking, it is true that very clayey soils are also very compact. They may be hard and dry or dense and plastic, according to the weather conditions. It is particularly true in the case of soils which are created by deterioration of schists; their physical structure is practically always deficient (Delecour pers. com.).

(2) In basic clays the calcium-ions may exert a beneficial effect by limiting permeability and preventing endosmotic water uptake (Blower 1955) or ions might be required in certain quantities for dietary requirements, e.g. growth, development of the exoskeleton or other tissues, or other biochemical phenomena.

(3) The eggs of millepedes are protected by a sticky secretion to which soil particles adhere. *Glomeris* coats the egg with soil (clay?) from the rectum (Blower 1955).

(4) It has been shown by Touchot, Kilbertus & Vannier (1983) that in the presence of clay minerals toxic phenolic substances in decaying oak leaves were adsorbed by phyllosilicates in the gut of the collembolan *Folsomia candida*. Also, in the presence of clay the combined action of microorganisms and collembolans was more efficient on hornbeam as well as oak leaves. These relationships have not been systematically studied in the case of millipedes.

It would be interesting to know more about the role of the four above-mentioned aspects in determining species distributions, and as biological phenomena. Such an approach requires that laboratory experiments and new field observations are carried out.

Therefore, future field observations will first concern the millepede community behaviour along a direct increasing gradient of soil clay percentage. Second, it will be necessary to complete such observations by ecophysiological studies made directly in the field, i.e. following recent trends in ecophysiological works (see Vannier 1983 and Bouché 1983, for discussion).

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Synopsis: *Original scientific paper*

KIME, R. D., & G. WAUTHY, 1984. Relationships between millepedes, soil clay percentage and mean annual temperature in deciduous forests. Pedobiologia **26**, 387—402

The study of distribution patterns of 20 species of millepedes in 19 deciduous forests in Belgium indicates that soil clay percentage and mean annual temperature have a good predictive value for numerical organization of communities. The heterogeneous nature of soil clay percentage (from 10.9% to 44%, in the present case) and local mean annual temperature (from 7.3 °C to 10 °C) accounts for a large proportion, at one and the same time, of the diversity and the spatial structure of communities. So, the millepedes seem to desert cold and heavy soil conditions; moreover, two species, i.e. *Blaniulus guttulatus* and *Leptoiulus kervillei*, can be regarded as "super-specialist" towards the four modes of habitat we may define from contrasted soil clay percentage and mean annual temperature conditions.

On the other hand, our study deals also with the predictive power of species on soil texture and local thermal phenomena.

Key words: community analysis, correspondence analysis, diversity, habitat preferenda, millepedes.